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A narrow window of summer temperatures associated with shrub growth in Arctic Alaska

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Abstract

Warming in recent decades has triggered shrub expansion in Arctic and alpine tundra, which is transforming these temperature-limited ecosystems and altering carbon and nutrient cycles, fire regimes, permafrost stability, land-surface climate-feedbacks, and wildlife habitat. Where and when Arctic shrub expansion happens in the future will depend in part on how different shrub communities respond to warming air temperatures. Here, we analyze a shrub ring-width network of 18 sites consisting of *Salix* spp. and *Alnus viridis* growing across the North Slope of Alaska (68–71°N; 164–149°W) to assess shrub temperature sensitivity and compare radial growth patterns with satellite NDVI (normalized difference vegetation index) data since 1982. Regardless of site conditions and taxa, all shrubs shared a common year-to-year growth variability and had a positive response to daily maximum air temperatures (Tmax) from ca. May 31 (i.e. Tmax ∼6 °C) to early July (i.e. Tmax ∼12 °C), two-thirds of which were significant correlations. Thus, the month of June had the highest shrub growth-temperature sensitivity. This period coincides with the seasonal increase in temperature and phenological green up on the North Slope indicated by both field observations and the seasonal cycle of NDVI (a proxy of photosynthetic activity). Nearly all of the sampled shrubs (98%) initiated their growth after 1960, with 74% initiated since 1980. This post-1980 shrub-recruitment pulse coincided with ∼2 °C warmer June temperatures compared to prior periods, as well as with positive trends in shrub basal area increments and peak summer NDVI. Significant correlations between shrub growth and peak summer NDVI indicate these radial growth patterns in shrubs reflect tundra productivity at a broader scale and that tundra vegetation on the North Slope of Alaska underwent a greening trend between 1980 and 2012.

1. Introduction

Shrub expansion across Arctic and alpine tundra ecosystems has been documented in recent decades using ground estimates of vegetation cover, dendrochronology, repeat aerial photography, and satellite remote sensing (Goetz *et al* 2005, Tape *et al* 2006, Myers-Smith *et al* 2011, 2015a, Frost and Epstein 2014, Hobbie *et al* 2017, Myers-Smith and Hik 2018). This expansion includes both increased shrub

biomass and establishment in new areas (Myers-Smith *et al* 2011, Tape *et al* 2012), and likely contributes to the large-scale increase in photosynthetic activity across the biome inferred from satellite observations (Goetz *et al* 2005, Bhatt *et al* 2010, Guay *et al* 2014, Ju and Masek 2016). Inter-annual variations in remotely-sensed observations of photosynthetic activity have been linked to inter-annual variations in shrub ring growth (Forbes *et al* 2010, Blok *et al* 2011b, Macias-Fauria *et al* 2012, Weijers *et al* 2018b), while

other studies have linked shrub growth with annual fluctuations of plant biomass at the community level (Milner *et al* 2018, Le Moullec *et al* 2019). Shrub expansion can cause feedbacks that drive further changes in climate related to surface albedo, as well as by modification of the carbon and hydrological cycles via alterations in permafrost, water balance, nutrient cycling and snow cover (Chapin *et al* 2005, Hinzman *et al* 2005, Sturm *et al* 2005, Hallinger *et al* 2010, Jespersen *et al* 2018). Arctic shrub expansion is also facilitating movement of boreal wildlife into the tundra biome (Christie *et al* 2014, Tape *et al* 2016a, 2016b).

Arctic shrub expansion implies enhanced growth of erect forms of *Salix* spp., *Betula* spp., and *Alnus* spp. in relatively warmer, wetter Arctic regions (Myers-Smith *et al* 2011) and dwarf shrub growth in the High Arctic (Weijers *et al* 2017, Buchwal *et al* 2019). Over the last several decades, summer warming has been associated with an increase in shrub cover and height in the Arctic (Tape *et al* 2006, Fraser *et al* 2011), and observations from experimental warming of tundra vegetation indicate enhanced shrub growth (Demarco *et al* 2014). Overall, continued shrub expansion may be expected in a warmer Arctic (Walker *et al* 2005, Raynolds *et al* 2008, Beck *et al* 2011), but the potential controls for such expansion across the Arctic are not well understood (Martin *et al* 2017).

Determining the growth response of Arctic shrubs to recent climate change and identifying the seasonal window that affects their growth are key to understanding their physiological limitations and for predicting vegetation feedbacks. One way to do this is to measure the annual radial growth of shrubs using dendrochronological techniques (Myers-Smith *et al* 2015b), and then identify the key climatic controls on these growth records (Hughes 2002). Myers-Smith *et al* (2015a) used dendroecological data on shrub growth from 37 sites across the Arctic and alpine tundra and showed that growth response to climate varies by geographic location, site conditions and species. Highly variable sensitivity of shrub radial growth to summer temperatures was reported at a pan-Arctic scale with higher positive responses in Eurasia than in North America, and with very heterogeneous responses in Alaska including negative, positive, and non-significant sensitivities (Myers-Smith *et al* 2015a).

Site conditions can affect the climate sensitivity of Arctic shrubs. For example, warming-induced shrub expansion and enhanced growth can occur in places where permafrost thaw has lead to warmer, better drained, and less acidic soils (Lawson 1986, Walker 1996, Jones *et al* 2013). In northern Alaska, Tape *et al* (2012) found that shrub expansion occurred in response to climate warming at sites with relatively warm and well-drained soils. In contrast, at adjacent sites with poorly drained soils, shrub growth rates and cover were relatively insensitive to

temperature variability. Water stress may also intervene to limit Arctic shrub growth in a warming climate (Ackerman *et al* 2017, Gamm *et al* 2018). Given the site-specific modulation of shrub-climate sensitivity and the highly variable results across the Arctic (Myers-Smith *et al* 2015a), exactly where and when Arctic shrub expansion will occur in the future in response to amplified high-latitude warming remains unknown.
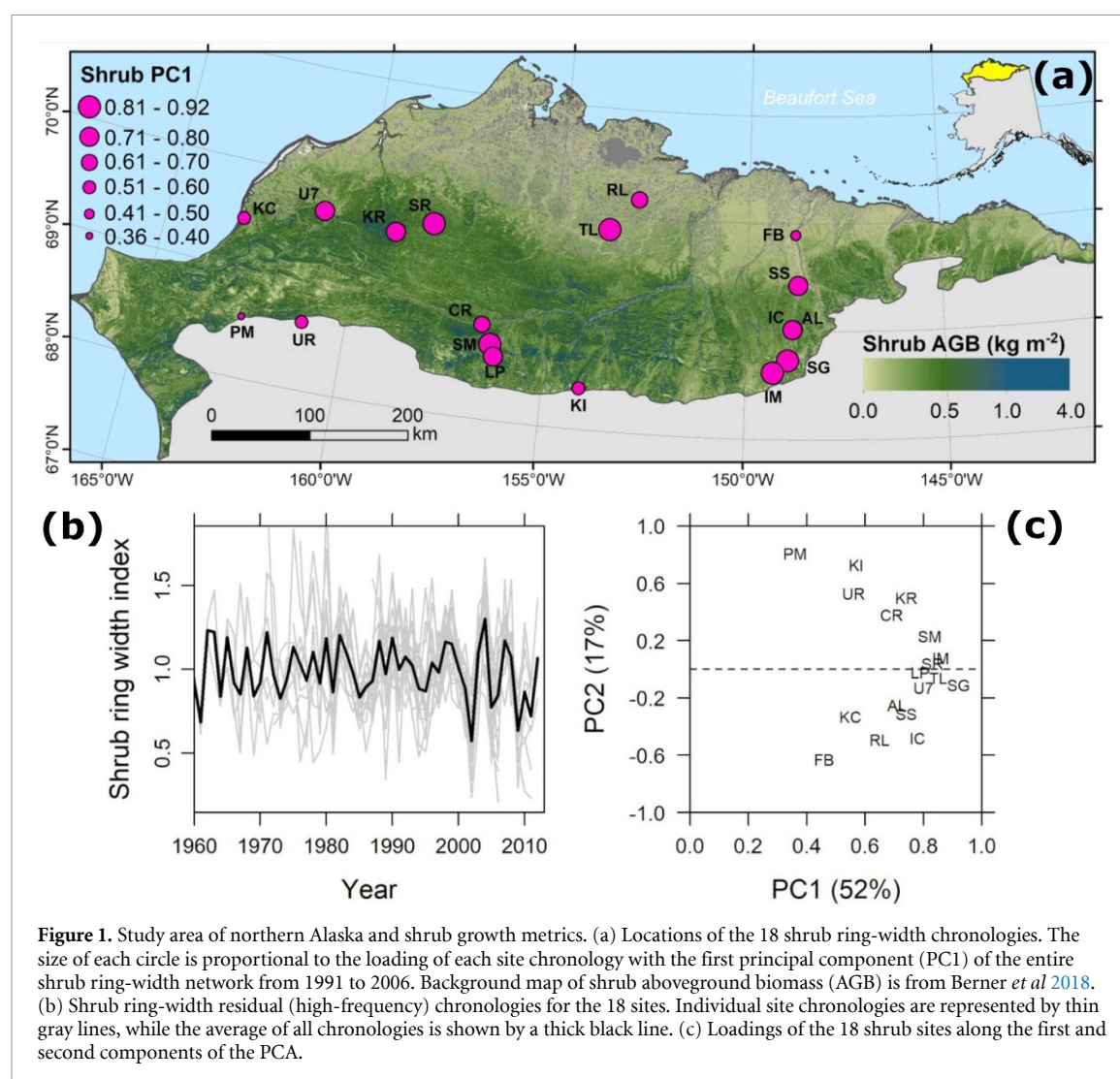
Satellite indicators of photosynthetic activity such as NDVI (Normalized Differenced Vegetation Index) are useful for studying tundra vegetation productivity. These data indicate positive trends or 'greening' across much of the Arctic, whereas declines in photosynthetic activity or 'browning' have been reported for some boreal forests in North America (1981–2003; Goetz *et al* 2005), and more recently short-term browning events have been reported in some tundra areas (Bhatt *et al* 2013, Bieniek *et al* 2015, Epstein *et al* 2015, National Academies of Sciences 2019). Satellite-based greening patterns have been heterogeneous across the Arctic, and particularly on Alaska's North Slope (1982–2008, Beck and Goetz 2011; 1982–2005, Goetz *et al* 2007). Recent advances using remote sensing with higher spatial resolution have confirmed widespread Arctic greening associated with warming air temperatures (Berner *et al* 2020) and growing season length (Arndt *et al* 2019). Nevertheless, spatial patterns of greening are not always consistent among sensors (Guay *et al* 2014) and there are numerous complexities with interpreting and attributing these satellite observations to actual ground-based biological processes (Myers-Smith *et al* 2020). Dendrochronological analyses of Arctic shrubs can provide a retrospective ground-based validation of the available satellite records, which is one of the goals of this study.

Here, we investigate the temperature sensitivity of shrub growth across the North Slope of Alaska based on ring-width chronologies and NDVI data from 18 sites. We targeted this region because it is an area where multiple satellite time series indicate strong greening in recent decades (e.g. Guay *et al* 2014). Specifically, we addressed the following research questions: (1) To what extent was inter-annual variability in shrub growth synchronous across the North Slope of Alaska? (2) Was there a common link between shrub growth and temperature across sites, and if so, what portion of the growing season was important for shrub growth? (3) How closely did satellite NDVI observations track inter-annual variability in shrub growth?

2. Materials and methods

2.1. Study area
The North Slope of Alaska extends from the Brooks Range north to the Arctic Ocean (figure 1(a)) and is dominated by tundra vegetation that primarily

Figure 1. Study area of northern Alaska and shrub growth metrics. (a) Locations of the 18 shrub ring-width chronologies. The size of each circle is proportional to the loading of each site chronology with the first principal component (PC1) of the entire shrub ring-width network from 1991 to 2006. Background map of shrub aboveground biomass (AGB) is from Berner *et al* 2018. (b) Shrub ring-width residual (high-frequency) chronologies for the 18 sites. Individual site chronologies are represented by thin gray lines, while the average of all chronologies is shown by a thick black line. (c) Loadings of the 18 shrub sites along the first and second components of the PCA.

consists of *Eriophorum vaginatum*-dominated moist acidic tussock tundra, and sedge- and sub-shrub-dominated moist non-acidic tundra (Raynolds *et al* 2005). Stands of upright shrubs of dwarf birch (*Betula* spp.), alder (*Alnus viridis*), and willow (*Salix* spp.) occur in a variety of settings: floodplains and water-tracks, lake shorelines, patterned ground ridges and troughs, and other disturbed or favorable sites with relatively deep active layers (the uppermost soil layer in permafrost terrain that thaws each summer). Sporadic shrub patches also occur on upland inter-fluves, especially in the warmer regions of the North Slope.

2.2. Shrub sampling
We collected shrubs from 18 sites on the North Slope between 2007 and 2014 (table 1; figure 1(a)). Most sites were visited as part of a regional paleoclimate project that included low-replication sampling of living willows for stable isotope analysis (Gaglioti *et al* 2017). For the current study, we supplemented these regionally extensive data from remote areas with intensive sampling at several more accessible locations. Ultimately, at each site, we collected basal stem cross sections from the largest willow or alder

shrubs within an area of 2–10 hectares, from 2 to 28 individual shrubs per site for a total of 284 radii from 140 individuals (c.f. table 1). To avoid sampling clones of the same individual, we collected cross sections from plants that were at least three meters away from one another. Despite low sample replication at a number of the remote sites, we included measurements from these sites to strengthen our insights into regional shrub growth dynamics.

2.3. Shrub ring-width chronology development
Individual shrub ring-width chronologies were generated using standard dendrochronological methods (Stokes and Smiley 1968). These included surface sanding, matching of growth patterns through visual cross-dating, measuring the ring widths to the nearest 0.001 mm, and statistically cross-dating using the software COFECHA (Holmes 1983). At least two radii were measured per sample (table 1). If severely eccentric growth was present and a radius showed several wedged or missing rings, only those radii with minimal eccentricity and without wedged rings were measured.

Each individual raw shrub ring-width series (figure S1 (see 'Data Availability Statement')) was

Table 1. Location and site characteristics of the 18 shrub ring-width chronologies: Latitude (Lat), Longitude (Lon), site characteristics, shrub species, number of radii and shrubs, mean ring width (10^{-2} mm) with standard deviation (STD) and first order autocorrelation (AR1). *Salix* spp. indicates that shrub samples consisted of either *Salix pulchra, S. glauca* or *S. alaxensis*.

Sites	Lat (oN)	Lon (oW)	Site characteristics	Shrub species	Timespan	Nº radii	Nº shrubs	mean	STD	AR1
AL	69.0	148.8	Slope over small hill, near 'Ice Cut' (Dalton Highway)	*Alnus viridis*	1920–2010	31	17	0.62	0.35	0.45
CR	68.9	156.6	Floodplain of Colville River	*Salix alaxensis*	1965–2011	5	2	0.17	0.09	0.21
FB	69.9	148.8	Holocene terrace of Sagavanirktok River	*Salix lanata* and *Salix alaxensis*	1986–2012	10	5	0.59	0.31	0.29
IC	69.0	148.8	Flat terrain next to Sagavanirktok River, near 'Ice Cut' (Dalton Highway)	*Salix* spp.	1977–2010	40	20	1.09	0.47	0.48
IM	68.6	149.3	Riparian corrdidor of stream at Imnaviat Creek	*Salix alaxensis*	1979–2012	14	5	0.59	0.30	0.37
KC	69.5	163.0	Watertrack near Chuk-chi Sea coast	*Salix* spp.	1975–2006	6	3	0.24	0.14	0.56
KI	68.4	154.1	Floodplain of Killik River	*Salix alaxensis*	1986–2011	12	6	0.35	0.18	0.51
KR	69.6	159.1	Water track near Ketik River	*Salix* spp.	1970–2007	8	4	0.34	0.13	0.46
LP	68.6	156.3	Snowpatches and water-tracks near Etivluk River	*Salix pulchra* and *Salix lanata*	1968–2011	24	12	0.40	0.16	0.48
PM	68.6	162.6	Water track on Poko Mountain	*Salix* spp.	1980–2006	8	4	0.33	0.13	0.35
RL	70.2	152.9	Floodplain of Judy Creek	*Salix alaxensis*	1991–2011	9	4	0.27	0.14	0.35
SG	68.7	148.9	Flat terrain near the Dalton road	*Salix* spp.	1964–2010	55	28	0.39	0.22	0.40
SM	68.7	156.4	Upland watertrack on Smith Mountain	*Salix pulchra* and *Salix lanata*	1974–2011	11	4	0.42	0.17	0.22
SR	69.7	158.2	Watertrack on Shanin-goruk Ridge	Salix spp.	1955–2006	9	5	0.19	0.09	0.59
SS	69.4	148.7	Upland watertrack and inter-fluve near Sagav-arnirktok River	*Salix pulchra* and *Salix lanata*	1987–2012	16	8	0.55	0.26	0.27
TL	69.9	153.6	Floodplain of Topo-goruk River	*Salix alaxensis*	1971–2006	6	3	0.30	0.11	0.38
U7	69.7	161.0	Floodplain of Lower Utukok River	*Salix alaxensis*	1980–2006	10	5	0.36	0.15	0.48
UR	68.6	161.1	Floodplain of Upper Utukok River	*Salix alaxensis*	1981–2011	10	5	0.82	0.41	0.31

detrended using a 15-year cubic smoothing spline (figure S2), which was chosen for the short time span of some of the time series, and an autoregressive model was applied to remove autocorrelation in the time series (Cook and Kairiukstis 1990). This process yielded individual residual, high frequency ring-width series that were averaged to generate a shrub ring-width chronology for each site (figure 1(b)). The Expressed Population Signal (EPS), a statistic ranging from 0 to 1 that measures the amount of shared variability among series within a chronology, was calculated for the common period of individual series for each of the 18 shrub chronologies (table S1, figure S3). We did not exclude chronologies that had EPS values below the arbitrary

0.85 cutoff (Wigley *et al* 1984) because we wanted to avoid losing spatial representativeness of our widespread network and because excluding these chronologies did not substantially change our results (see section 3.2).

Raw ring-width shrub data were used to calculate basal area increments (BAI) for each individual shrub (figure S4). We used the first year of growth (calendar year of the pith) as an estimation for shrub establishment or recruitment (figure S5). We are aware that this method does not always provide an exact germination date for shrubs with multiple stems since unsampled ramets (live or dead) may represent older growth episodes of an individual. Chronology development and statistics were made using the dplR

package (Bunn 2008) in R statistical software (R Core Team 2018).

2.4. Coherence of the shrub ring-width network
We assessed the regional coherence in inter-annual variability across the shrub ring-width network with Principal Components Analysis (PCA), using the Psych package in R (Revelle 2018). The PCA was performed on the 18 residual shrub ring-width chronologies for the common period from 1991 to 2006. A regional shrub chronology was also developed by averaging the 18 site chronologies (table S1) with different numbers of site chronologies in the first and last years due to their distinct time spans.

2.5. Relationships between shrub growth and climate
To assess the influence of air temperature on shrub growth, we correlated the standard ring-width site chronologies (figure S2) with gridded CRU TS4.03 monthly maximum air temperature (Tmax; Harris *et al* 2014) and daily maximum, minimum, and mean air temperatures based on Sheffield *et al* (2006) climate datasets. Monthly correlations from the September prior to the year of ring formation to the September of the year of ring formation were computed for each site. In addition, daily maximum and minimum temperatures from the Sheffield dataset were averaged every 10 days and correlated with the shrub series from the first (May 11–20) to the last (August 29–September 9) 10-day windows of the growing season. Correlation between residual ring-width site chronologies and pre-whitened and detrended Tmax values were also computed for the 10-day windows to discard potential artifacts related to ring-width detrending. Analyses were repeated for the same time intervals using the regional shrub chronology and the first (PC1) and second (PC2) principal components of the shrub-ring network. Correlation analyses were performed using the Treeclim package in R (Zang and Biondi 2015). The level of significance of the correlation coefficients was assessed by bootstrap correlation analysis (Politis and Romano 1994).

2.6. Temperature trends
To assess the significance of the warming trends at the 18 sites, linear regression analyses were performed on air temperature data interpolated for the grid cells ($0.5°\times0.5°$ resolution) of each shrub sampling location for time intervals beginning in 1900, 1960 and 1980. Air temperature data included daily means of 10-day periods starting on May 31, June 10, June 20 and June 30 (time intervals exhibiting the highest correlations between growth and climate). The same analyses were performed for the entire May 31 to July 9 period. Probability distribution functions and the Kolmogorov-Smirnoff test were used to assess if temperatures for the periods before and after 1980 were significantly different ($P < 0.05$).

2.7. Relationship between shrub growth and GIMMS$_{3g}$ NDVI
Annual shrub growth indices were correlated with NDVI time series from the third generation of the Global Inventory Modeling and Mapping Studies (GIMMS$_{3g}$) data set (Pinzon and Tucker 2014) derived from satellite observations from the Advanced Very High-Resolution Radiometers (AVHRR). NDVI is a proxy for canopy light absorption and photosynthetic capacity (Tucker and Sellers 1986). GIMMS$_{3g}$ NDVI (hereafter referred to as NDVI) has a spatial resolution of $\sim$8 km $\times$ 8 km and observations extend from mid-summer 1981 to present at a bi-weekly cadence. We acquired these data from the NASA Earth Exchange and extracted the NDVI time series for each sampling site using the raster package in R (Hijmans 2017). Each of the 18 chronologies was then correlated with detrended and pre-whitened, bi-weekly NDVI data from May 15 to September 30 and with cumulative and maximum NDVI during that seasonal window. The analyses were then repeated for each site using the BAI chronologies and NDVI data without detrending and pre-whitening. To assess regional correspondence between shrub growth and NDVI, each timeseries was averaged across all 18 sites and the resulting timeseries were correlated. We anticipated positive correlations between shrub growth and NDVI (e.g. Weijers *et al* 2018b), thus we evaluated the statistical significance of these correlations using one-sided, upper tail t-tests.
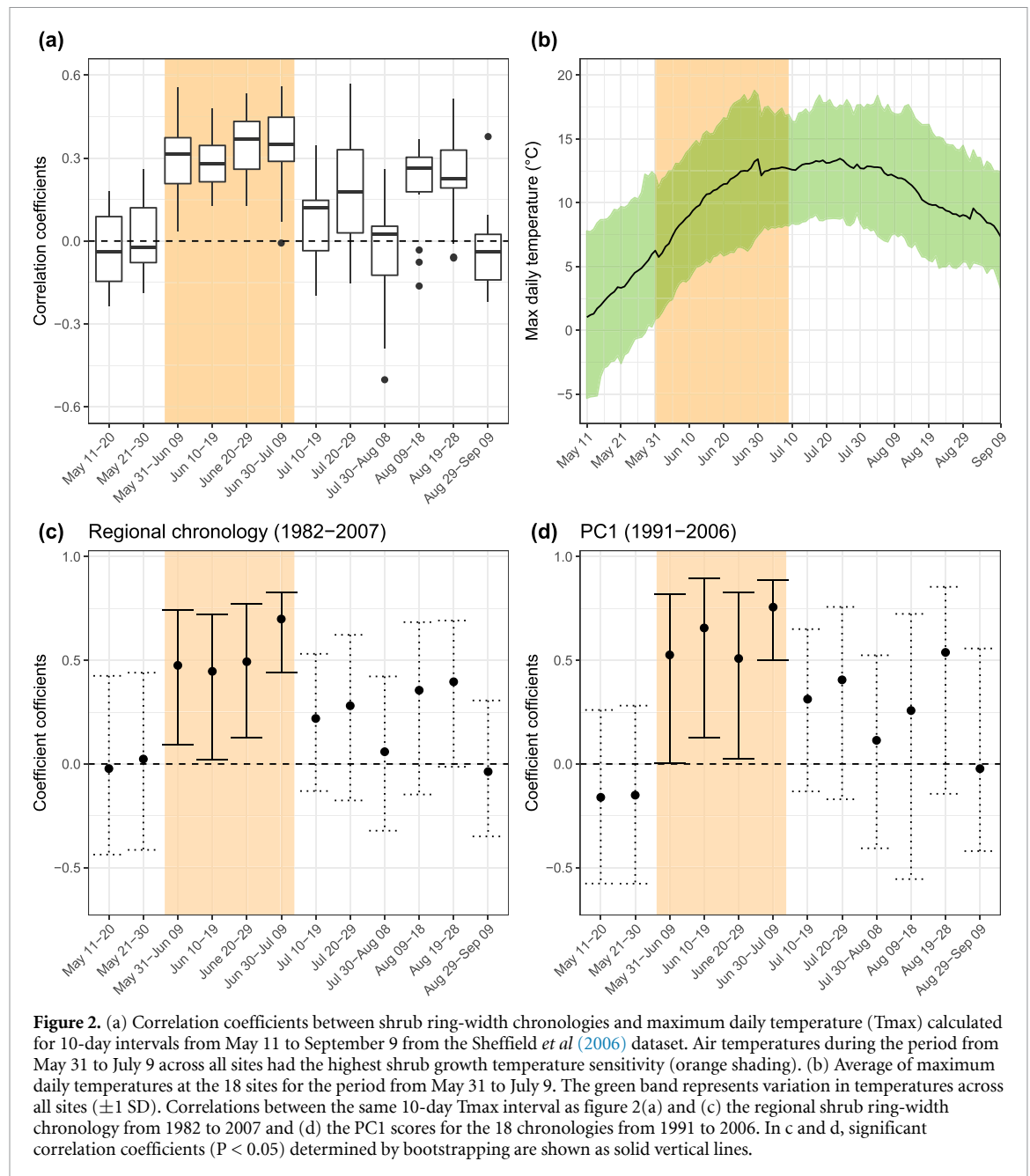
2.8. Shrub growth during the warmest and coldest years since 1982
The three warmest and the three coldest years from 1982 to 2012 (i.e. the lowest and highest deciles for this 30 year period) during May 31 to July 9 were selected from the average of the Tmax data for all the sites. We then tested whether mean shrub RWI and BAI anomalies, raw Maximum NDVI and pre-whitened and detrended Maximum NDVI differed between the coldest and warmest years using Wilcoxon rank sum test.

3. Results

3.1. Regional coherence of shrub growth
The 18 shrub ring-width residual chronologies (figure 1(b)) were used to assess growth coherence both within and among sampling sites (figure 1(a)). The mean correlation among shrub individual growth series within each site averaged 0.45 with a maximum value of 0.72 (table S1). The PC1 and PC2 accounted for 52% and 17%, respectively, of the regional variance in shrub growth chronologies. All ring-width residual chronologies (pre-whitened inter-annual indices) shared common growth variability (positive PC1 loadings; figure 1(c)). Even chronologies with low EPS values

Figure 2. (a) Correlation coefficients between shrub ring-width chronologies and maximum daily temperature (Tmax) calculated for 10-day intervals from May 11 to September 9 from the Sheffield *et al* (2006) dataset. Air temperatures during the period from May 31 to July 9 across all sites had the highest shrub growth temperature sensitivity (orange shading). (b) Average of maximum daily temperatures at the 18 sites for the period from May 31 to July 9. The green band represents variation in temperatures across all sites (± 1 SD). Correlations between the same 10-day Tmax interval as figure 2(a) and (c) the regional shrub ring-width chronology from 1982 to 2007 and (d) the PC1 scores for the 18 chronologies from 1991 to 2006. In c and d, significant correlation coefficients (P < 0.05) determined by bootstrapping are shown as solid vertical lines.

showed positive loadings on PC1, indicating a common agreement in inter-annual variability among shrub growth across the North Slope of Alaska (figure 1; table S1). Regarding PC2, site chronologies exhibited both positive and negative loadings (figure 1(c); table S1).

3.2. Shrub growth response to air temperatures

Shrub radial growth showed an overall positive response to summer monthly Tmax (site level: figure S6; regional average: figure S7(a)) for the period between 1980 (or first available year) and the last year of each chronology (table S1). Air temperature in June had the highest correlations with shrub growth and the least variability in correlation strength among sites (r = 0.38 $\pm$ 0.09; mean ± 1 SD) with all site chronologies showing positive correlation

coefficients, ~56% of which were significant (table S2(a); figure S7(a)). Mean correlation coefficients for July and August Tmax ranked second and third in summer (mean r = 0.22 and 0.17, respectively) and showed much higher variability in correlation strength among sites (SD = 0.18 for both). Correlation coefficients with previous October and November Tmax had similar mean and SD than correlation coefficients with current year July and August Tmax. Similar correlations between shrub growth and monthly air temperature were found using CRU data for the region extending from 68–71°N and 164–149°W (figure S7(b); table S2(b)). The correlations between shrub growth and temperature were more variable outside the growing season, with some sites exhibiting negative correlation coefficients with temperature during previous winter months (e.g.
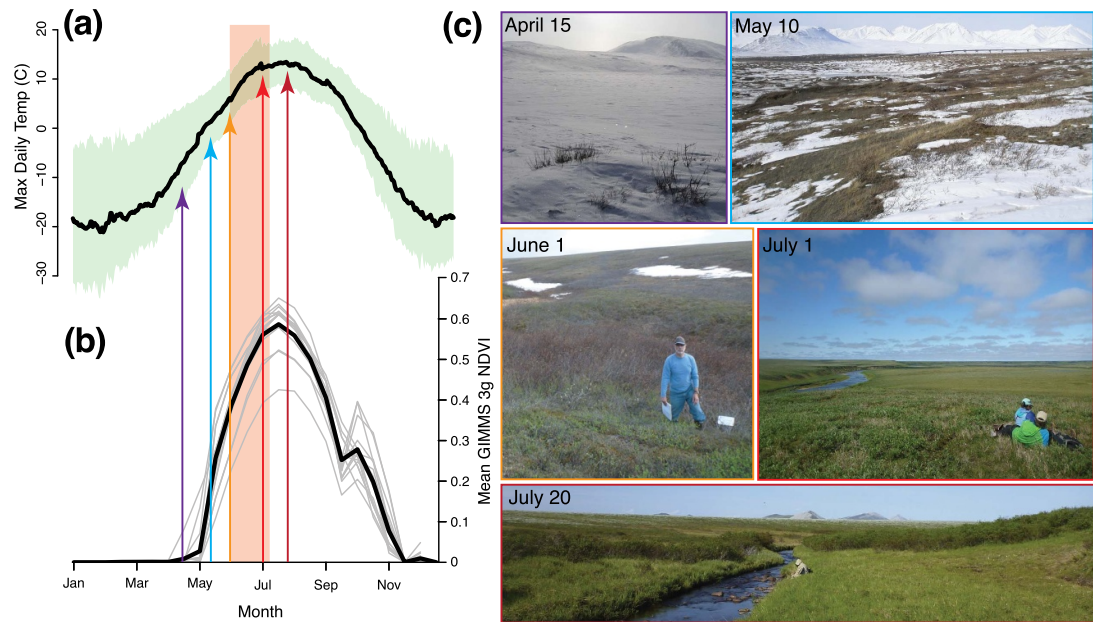
Figure 3. (a) Seasonal cycles of maximum daily temperature and (b) GIMMS$_{3g}$ NDVI using data averaged from 1980 and 1982, respectively, through 2012. (c) Photos taken at various locations on the North Slope that represent seasonal snapshots of shrub phenology. The orange band in (a) and (b) shows the critical time window of shrub-temperature sensitivity and the vertical arrows indicate the periods when the photos in (c) were taken.

January and February), as well as at the end of the season in September and to a lesser degree in March and May (figures S7(a) and (b); tables S2(a) and (b)). Similar growth-temperature correlation results were obtained using daily minimum temperature (results not shown).

Maximum daily air temperature between May 31 and July 9 exerted the strongest control on shrub growth (figure 2(a)). These four 10-day intervals showed the highest correlations (r = 0.28–0.36) and the maximum number of chronologies with positive (94%–100%) and significant (∼33%–56%) correlation coefficients (table S3(a); figure S8). Moreover, using the mean Tmax during May 31 to July, all site chronologies showed positive correlations (r = 0.42 ± 0.14; mean ±1 SD), 66.7% of which were significant. Consistent results were also found when sites with lower EPS values were removed (figures S9(a) and (b)) and when correlating residual shrub ring-width chronologies and pre-whitened maximum temperatures (figure S9(c); table S3(b)).

Growth-temperature response at each site was less likely to be well reflected at sites with low sample size and low EPS values (table S1; figure S3), thus it is unclear whether climate sensitivity (tables S2, S3) would have been the same or higher if some sites had more shrub samples. Despite this caveat, the combined site-specific correlation coefficients (figure 2(a)) expressed a regional shrub response that showed a coherent temperature sensitivity during this

particular time window across all sites (table S3(a)). This pattern was corroborated when the regional chronology (figure 2(c)) and PC1 scores (figures 2(d) and S10(a)) were correlated with the same 10-day windows of Tmax. On the other hand, the PC2 scores showed negative correlations with Tmax during the second half of July (figure S10(b)). We also acknowledge that although the overall correlation patterns remain the same, the significance levels (P < 0.05) assessed by bootstrapping procedures varied slightly for some correlation coefficients among different computation runs (see figures 2(d) versus S10(a)). Based on these results, air temperature in June, along with the first ten days in July, emerged as the time window in which shrub radial growth was most sensitive to temperature on the North Slope of Alaska.

3.3. Seasonality of temperature and NDVI during the sensitive time-window for shrub growth
The peak sensitivity window for shrub radial growth spanned the period from May 31 to July 9 (figure 2(a)), beginning when daily Tmax reached ∼6 °C, continued with the seasonal increase in temperature, and ended in early July when Tmax plateaued at around ∼12 °C (figures 2(b) and 3(a)). This sensitive time window for shrub growth also typically coincides with shrub green-up after snow-melt on the North Slope, as illustrated by both the NDVI seasonal cycle (figure 3(b)) and on-the-ground observations (figure 3(c)).
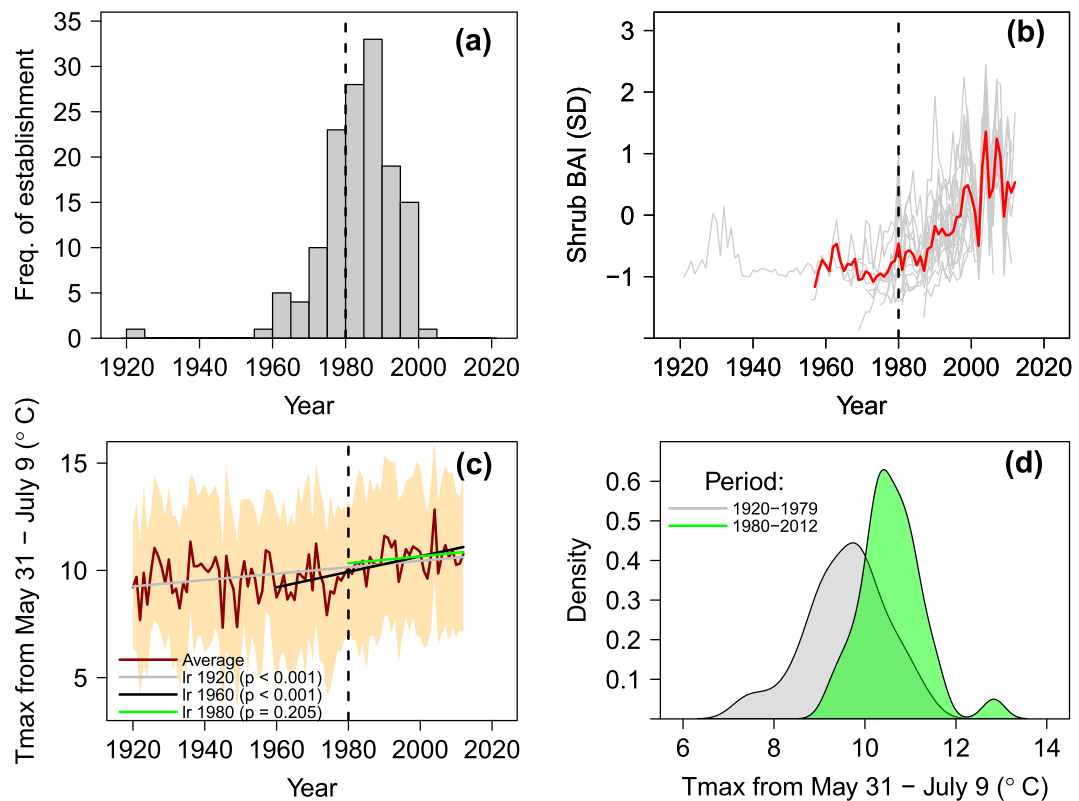
Figure 4. (a) Timing of stem initiation for sampled shrubs across the 18 study sites. Shrub stems primarily established since the 1960s (~74% since 1980). (b) Standardized (SD) shrub basal area increment (BAI) time series for each sampling site. The red line indicates the average BAI across all sites. (c) Mean daily maximum air temperature (Tmax) across the 18 sites for the critical period of growth (May 31 to July 9) since 1920. Significance of the warming trends were assessed through linear regression (lr) since 1920, 1960 and 1980. (d) Probability density functions for Tmax before and after 1980, highlighting significantly warmer conditions in the more recent period (p < 0.001).

### 3.4. Stem establishment, shrub growth trends, and climate warming

Nearly all (98%) of the sampled shrub stems established after 1960, with most (74%) establishing after 1980 (figure 4(a)). Larger BAIs were also found after 1980 for the 18 sites, and were even larger after 2000 when a higher coherent growth across sites was observed (figures 4(b)). Note that a portion of these increasing trends could likely be due to positive age-size trends associated with the BAI timeseries (the average age of the sampled shrubs was 26 ± 10 years; mean ±1 SD).

June temperatures after 1980 were up to ~2 °C warmer than before (figure 4(c) and (d)). This coincided with pronounced recruitment of shrubs and the onset of increasing BAI. Mean BAI and peak NDVI anomalies significantly (P < 0.05) increased at 16 of 18 sites between 1980 or 1982 and the last year of growth measured at the site (tables S4 and S5). Tmax from May 31 to July 9 did not show a significant positive trend since 1980, but significant warming trends were detected since 1920 and 1960. The period after 1980 was also significantly warmer than the rest of the 20th century based on probability density functions and the Kolmogorov-Smirnoff test (figure 4(d)). These results were consistent when Tmax was analyzed for individual sites from May 31 to

July 9 (figure S11) and when the four 10-day intervals from May 31 to July 9 were analyzed separately (figure S12).

3.5. Relationships between shrub radial growth and GIMMS$_{3g}$ NDVI

Correlations between shrub ring-width chronologies and NDVI were typically weak, and mostly insignificant, when both series were detrended and pre-whitened (figures 5(a), (b) and S13). The residual shrub-ring chronologies exhibited the strongest correlation with NDVI collected during the second half of June and first half of July, when 28%–33% of the sites showed significant but weak correlation (mean r = 0.22, P ⩽ 0.05; figure 5(a)). However, correlations between shrub BAI anomalies and NDVI were stronger than those between detrended and pre-whitened shrub ring-width chronologies and NDVI (figures 5(c) and (d)), even though the seasonal pattern of correlations was similar (figures 5(c) and (d) versus figures 5(a) and (b)). Similar to RWI-NDVI relationships, BAI exhibited the strongest correlation with NDVI from the second half of June through July, when 72%–78% of sites showed significant correlations (mean r = 0.44 to 0.52; figure 5(c)). Maximum NDVI occurred in July and had the highest correlations with residual RWI and BAI
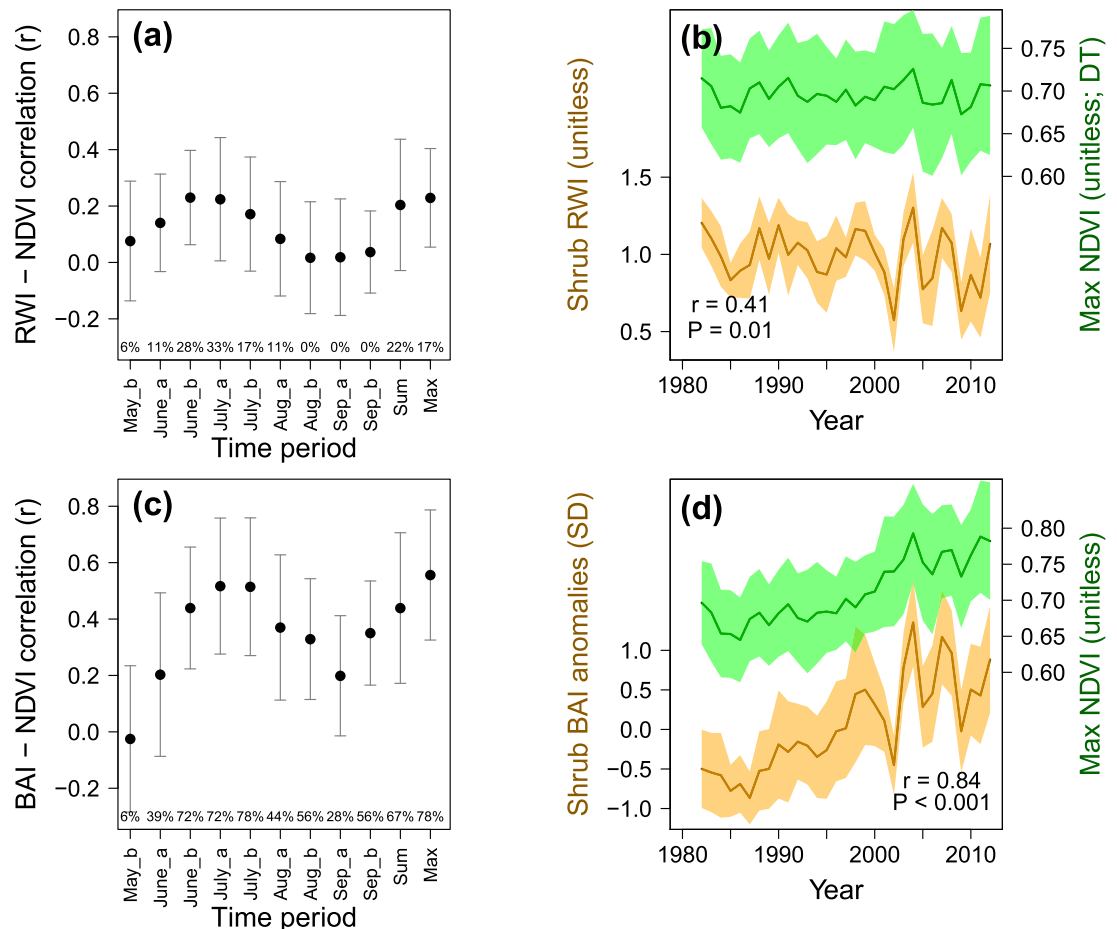
Figure 5. Relationships between annual shrub growth and the normalized difference vegetation index (GIMMS$_{3g}$ NDVI) derived from AVHRR satellite data. (a) Mean correlation (±1 SD) between average shrub residual ring-width index (RWI) and bi-weekly NDVI from 1982–2012 across the 18 shrub sampling sites. Both series were detrended and pre-whitened prior to computing correlations. The percentage of sites that exhibited a significant (P ⩽ 0.05) correlation between RWI and bi-weekly NDVI is also provided. (b) Shrub RWI and detrended max NDVI from 1982–2012 averaged (±1 SD) across all shrub sampling sites. (c) and (d) same as (a) and (b) but with mean standardized (SD) shrub basal area increment (BAI) anomalies versus NDVI without detrending or pre-whitening either time series.

timeseries, which averaged 0.23 and 0.56, respectively (figures 5(a) and (c)).

In contrast to site-level comparisons, the correlations between shrub growth and maximum NDVI were stronger when measurements were averaged across the 18 sampling sites to represent regional shrub-growth and photosynthetic activity (figures 5(b) and (d)). Regionally-averaged shrub ring-width chronologies and max NDVI (detrended and pre-whitened) were positively correlated (r = 0.41, P = 0.01; figure 5(b)), but again the association was stronger when regionally-averaged shrub BAI anomalies were compared with max NDVI that was not detrended or pre-whitened (r = 0.84, P < 0.001; figure 5(d)). The stronger correlation between shrub BAI and NDVI relative to the detrended pre-whitened data arose because both regionally-averaged shrub BAI and NDVI exhibited a strong positive trend from 1982 to 2012 (+0.05 BAI SD yr^{-1}, r^2 = 0.65, P < 0.001 and +0.004 NDVI yr^{-1}, r^2 = 0.78, P < 0.001). Note that we found similar

results when we excluded sites with EPS values lower than 0.75 and 0.85 (figure S13).

Finally, during the years that had the warmest early summer periods (1990, 1991, 2004), significantly (P ≤ 0.05) higher RWI (figure S14(a)) and BAI (figure S14(c)) anomalies indicate enhanced shrub growth relative to the years with the coldest early summer air temperatures (1985, 1994, 2002). Higher NDVI values were also consistently found in these warmest years compared to the coldest years (figure S14(b) and (d)), just significant (P ≤ 0.05) in the detrended and pre-whitened NDVI series (figure S14(b)).

4. Discussion

4.1. Shrub growth response to June temperatures
Our results reveal a strong, coherent signal among the shrub radial growth patterns (i.e. >50% explained variance of PC1) that was independent of site characteristics. In other words, shrubs across the

North Slope of Alaska from a wide range of site conditions and taxa share a common growth signal and appear to have been affected by a common environmental factor. Our results demonstrate that June and early July temperatures exert the strongest control on *Alnus viridis* and upright *Salix* spp. radial growth across the North Slope of Alaska. Warm temperatures in the second half of July, August, and the previous Fall (October and November) also enhance shrub growth but less so than during June and early July. This high sensitivity to early summer temperatures agrees with results reported at other sites on the North Slope (Ackerman *et al* 2017, 2018) and in expanding alder patches across Arctic Alaska (Tape *et al* 2012), where significant correlations between alder growth and prior November temperatures were also found. Elsewhere in the Arctic, early summer temperatures have also been found to be the most important climatic factor affecting *Salix pulchra* and *Betula nana* radial growth in northeastern Siberia (Blok *et al* 2011a) and *S. pulchra* in the Yukon (Canada) at 61° N (Weijers *et al* 2018b). While temperatures at the onset of the growing season have a strong influence on shrub radial growth at all sites, we found that mid-summer temperatures may drive moisture stress in about half of the shrub sites. This is shown by the positive association between these sites and the PC2, which is negatively correlated to Tmax in the second half of July (figure S10(b)). Other factors such as permafrost thaw depth, soil temperature, nutrient availability, and plant water stress can also alter shrub-climate sensitivity (Tape *et al* 2012, Myers-Smith *et al* 2015a, Ackerman *et al* 2017, 2018). Although it was important for the last 35 years of shrub growth, the critical seasonal window detected here for the North Slope of Alaska (i.e. June-early July) may change as the phenology of Arctic vegetation shifts in response to warming temperatures.

Why might shrub growth be particularly sensitive to June air temperatures? On the North Slope of Alaska, June is the time when daily maximum air temperatures begin to reach ∼6 °C (figure 2(b)), which is consistent with the threshold between 5.5 °C and 7.5 °C documented for plant tissue growth at altitudinal treeline (Körner 1998). June temperatures might thus affect the onset and seasonal duration of photosynthesis and xylogenesis (Vaganov *et al* 2006). Furthermore, spring green-up of shrub tundra occurs during June, as indicated by the NDVI satellite data (figure 3(b)), our observations (figure 3(c)) and prior field studies in the region (Riedel *et al* 2005). Late June and July also correspond to the period with the highest incident radiation (Eugster *et al* 2000), when we observe the strongest coupling between shrub growth and NDVI (figure 5). These findings support the hypothesis that warmer temperatures during early summer increase the rate of leaf development and leaf area, thereby increasing canopy light absorption and

photosynthate production (e.g. Hudson *et al* 2011). This increase in photosynthates, coupled with high cambial activity that can be also associated to warmer June temperatures, may be enhancing radial growth (figure 2 and S14).

We also found that shrub growth was lower following warm winters (mainly after warmer temperatures in January and February). Extreme winter warming events and years with low snow accumulation have been shown to damage dwarf shrub vegetation in Scandinavia (Bokhorst *et al* 2008, Bjerke *et al* 2017). Warmer winters may also drive shifts in shrub phenology such as earlier bud burst and leaf unfolding in spring, which can increase the susceptibility of shrubs to frost damage (Inouye 2000, Rigby and Porporato 2008, Bokhorst *et al* 2009). In this context, we found some negative influence of early growing season temperatures (i.e. May) on growth, which has also been reported for shrub growth near treeline suggesting that early spring warming may advance bud burst and flowering, making plants vulnerable to subsequent spring frost events (Weijers *et al* 2018a). Together, these patterns suggest that shrubs may not necessarily benefit from warming that occurs outside the growing season.

4.2. Shrub stem recruitment

Most shrub recruitment occurred after 1980 at our study sites, but we acknowledge that the ecological meaning of this pattern has some caveats. First, our sampling was not designed to assess shrub recruitment because we only targeted the largest shrubs and ramets at each study site, and this subset may not necessarily represent the oldest individuals. Second, stem growth initiation (or first year of growth) is not always the same as shrub establishment, since an individual can have multiple stems and it is unclear how long an individual shrub lives due to the clonal character of a given species. Despite these uncertainties, relatively few shrubs were found to be growing at our sites before 1980, supporting the idea that the post-1980 period was likely a time of shrub expansion on the North Slope. Our data also showed significant positive trends in BAI after 1980, although potential age-related increases in growth complicate attributing higher growth rates to temperature alone.

This apparent pulse in shrub recruitment and the simultaneous increase in shrub BAI coincided with ∼2 °C warmer June temperatures after 1980. Thus, the post-1980 increase in June temperature may have enhanced shrub growth, and likely contributed to the widespread shrub expansion observed in repeated aerial photographs of the North Slope (Tape *et al* 2006, Naito and Cairns 2015). Advancement of altitudinal shrubline and increased shrub recruitment and growth following climate warming have also been reported in the Yukon (Canada), but with potentially different climate drivers (i.e. summer versus winter temperatures for growth and recruitment,

respectively) (Myers-Smith and Hik 2018). An association between temperature and recruitment has also been reported for earlier periods such as in the mid-20th century (e.g. East Greenland; Buntgen *et al* 2015). Overall, our results suggest a recruitment pulse and enhanced shrub growth after 1980 (figures 4(a) and (b)), which coincided with enhanced vegetation photosynthetic activity and the 'greening' observed by satellites (figures 3(b) and 5), as well as a rise in early summer temperatures (figure 4(d)).

4.3. Shrub growth and NDVI relationships

We found that the strength of the shrub growth-NDVI relationship depended on the spatial scale examined, and whether the comparisons focused on inter-annual variation or longer-term trends. In terms of spatial scale, the relationships between shrub growth (RWI or BAI) and summer NDVI were consistently stronger using regionally averaged rather than site-specific NDVI data. The lower site-specific co-variation is likely related to the mismatch in scale between the shrub sampling and the coarse spatial resolution NDVI data ($\sim$64 km^2 pixels) against which shrub growth was compared. In some cases, it may also be related to low shrub sample replication at certain sites. Not only might the shrub samples from a site not fully represent shrub growth at the site or across the entire NDVI pixel, but the NDVI signal integrates heterogeneous landscapes for which shrubs are but one component of the plant community and overall land surface (Epstein *et al* 2008, Berner *et al* 2018, Myers-Smith *et al* 2020). Averaging shrub growth and NDVI across the region likely reduces noise in each variable and enhances the climatic influence of the ground- and space-based measurements, leading to stronger correspondence between these two metrics (figures 5(b) and (d)). This finding is consistent with earlier work showing that *Salix lanata* radial growth in coastal northwestern Russia was more strongly correlated with regional than site-specific NDVI (Forbes *et al* 2010). This scale dependency highlights the importance of spatially extensive sampling when evaluating coarse-resolution satellite observations using field measurements.

Our analyses suggests that summer NDVI better tracks longer-term increases in shrub growth (BAI) than inter-annual variability in shrub growth (RWI). The shrub RWI time series were detrended and standardized to emphasize inter-annual variability in growth. We found modest positive correspondence between regional shrub RWI and detrended maximum summer NDVI (r = 0.41) during recent decades, which is consistent with prior studies focused on tundra shrubs in Russia (Forbes *et al* 2010, Blok *et al* 2011a, Macias-Fauria *et al* 2012) and Canada (Weijers *et al* 2018b), as well as on circumboreal trees (Berner *et al* 2011, Beck *et al* 2013, Bunn *et al* 2013). These moderate relationships partially emerge because shrub and tree RWI emphasize inter-annual

variability in stem growth, while NDVI is an indicator of canopy light absorption and photosynthetic capacity (Goetz and Prince 1999, Berner *et al* 2011). Neither RWI nor NDVI is a perfect proxy for plant productivity and the link between them is likely affected by inter-annual variation in plant respiration and allocation of photosynthates (cf. Milner *et al* 2018, Le Moullec *et al* 2019). On the other hand, we found a much stronger relationship between regional shrub BAI and non-detrended maximum summer NDVI (r = 0.84) during a period when both metrics markedly increased. Shrub BAI time series are more closely related to the absolute magnitude of annual growth (or aboveground net primary productivity) because this metric corrects for the geometrical constraints of decreasing ring width with increasing stem circumference. The stronger relationship between shrub BAI and NDVI likely reflects that the increase in shrub BAI was associated with increases in canopy leaf area and photosynthetic rates that contributed to a progressively 'greener' landscape. Overall our results, together with earlier studies (Forbes *et al* 2010, Blok *et al* 2011a, Macias-Fauria *et al* 2012), indicate that inter-annual variability and trends in summer NDVI are partly related to shrub growth in tundra regions.

5. Conclusions

We found that inter-annual variability in shrub radial growth was coherent across wide-ranging sites on the North Slope of Alaska. June temperatures appear to exert an important control on shrub growth and recruitment. Shrub growth was most sensitive to Tmax between May 31 and July 9 when Tmax ranged from $\sim$6 °C to $\sim$12 °C. This seasonal window coincided with the timing of green-up indicated by field observations and the annual rise in plant productivity (photosynthetic activity) expressed by NDVI. Our findings also link inter-annual variability and trends in NDVI with shrub growth, particularly at a regional scale, thus providing multiple perspectives on recent tundra vegetation dynamics. The fate of tundra shrub productivity, and possible Arctic shrub expansion into new areas, may depend on how rapidly this early summer period, which is critical for growth rates and recruitment, continues to warm, as well as the frequency of extreme winter warming events.

Acknowledgments

Data Availability Statement

The data that support the findings of this study are available from the ITRDB database at the NOAA server: AL (AK174 https://doi.org/10.18739/A2DV1CP5T), IC (AK175 https://doi.org/10.18739/A2930NW10) and SG (AK176 https://doi.org/10.18739/A2599Z273) and Arctic Data Center (ADC). The rest of the shrub datasets are available upon reasonable request from the BVG author.

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